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NEST ARCHITECTURE AND PEDOTURBATION OF *FORMICA OBSCURIPES* FOREL (HYMENOPTERA: FORMICIDAE)

Thomas J. McCahon and Jeffrey A. Lockwood
Department of Plant, Soil and Insect Sciences, University of Wyoming, Laramie, Wyoming 82071

Abstract.—A study of the pedobiology of *Formica obscuripes* Forel was conducted from May to September of 1988 in a montane meadow habitat in southeastern Wyoming. The selected study site afforded an undisturbed community of 38 viable ant nests ranging in size from 0.14 to 0.65 m^3, with populations of 9000 to 66,500 individuals. The populations and body sizes of the castes were determined. Foraging paths from the nests averaged 15.7 m in length and served as routes for the collection of food and thatching materials. The nests were 43% thatch, 35% soil and 22% gravel by weight, although nearly 50% of the nest volume was air space. As a result of the construction and materials, the nests were able to collect solar radiation and remain significantly warmer than the surrounding soil. This passive heating may have been actively enhanced by the behaviors of the ants when eggs were present. Compared to adjacent soil, the soil in the ant nests had more sand and less silt and clay, greater porosity, less moisture, and greater acidity.

Key Words.—Insecta, *Formica obscuripes*, pedoturbation, nest, thermoregulation

Formica obscuripes Forel was discovered in 1886 in Green River, Wyoming. The range of *F. obscuripes* is from Michigan to Oregon, with a southern extension into New Mexico (Gregg 1963, Wheeler & Wheeler 1986). This range has been extended since 1950, at which time the limitations were Illinois to Idaho, and reached only to southern Colorado (Creighton 1950). Altitudinal limits in the Rocky Mountains appear to be from 1070 to 2900 m asl (Gregg 1963). Habitats for nest sites are generally in open grasslands, devoid of cover (Wheeler & Wheeler 1963). The nest of this thatching ant is apparently composed primarily of dead vegetation, collected from the surrounding habitat (Cole 1932, Weber 1935). However, the manner in which the material is chosen, the inclusion of inorganic substances and the physical characteristics of the nest are largely unknown. In addition, little is known regarding interactions between nests or population dynamics within nests (Gregg 1963, Sather 1972).

This study was undertaken to quantitatively assess the characteristics of the thatching ant, *F. obscuripes,* and its nest, and their influences on a mountain meadow soil in the Laramie Mountains, Wyoming. Numerous studies have been conducted that give some indication of the bioturbation of soils by ants (e.g., Baxter & Hole 1967, Salem & Hole 1968, Wiken et al. 1976, Culver & Beattie 1983) but none of these studies included an ant species that uses a major nesting material other than soil for nest construction. Given the prominent size and unique construction of nests by *F. obscuripes* it appeared likely that they have a marked influence on the physical and chemical characteristics of the surrounding soil.

Materials and Methods

Study Site Description.—The study area was located southwest of Dirty Mountain (T17N, R72W, Sec. 35, NE¼) at an elevation of 2423 m in Rogers Canyon, Albany County, Wyoming. The soils in the area are Typic Argiborolls, developed on moderately sloping (10 to 25 degrees) Plutonic rocks (anorthosite complex) of Middle Proterozoic age. The study area was a 279 m^2 site on a moderately well drained east facing slope. Permeability at the site was moderately rapid, with soils being moist at the time of sampling. There was a change in slope of 3 m from the eastern edge of the study site to the higher western edge. Slope gravels and lithic contact in all nest locations of the study area restricted soil sampling to between 50 and 90 cm.

The study site was an alpine meadow, occasionally used for cattle grazing. The only trees, quaking aspen (*Populus tremuloides* Michaux) were located high on the eastern slope of the site. The area supported various grasses and forbs, including big bluestem (*Andropogon gerardi* Vitman), bluebunch wheatgrass (*Agropyron trachycaulum* (Link) Malte ex Lewis), vetch (*Vicia* spp.), wild mint (*Mentha arvensis* L.), bisquit-root (*Lomatium triternatum* (Pursh) J. Coulter & Rose), and wild onion (*Allium cernum* Roth). The meadow previously supported sagebrush (*Artemisia* spp.), as indicated by the presence of dried and decayed roots in most of the ant nests.

The mean total annual precipitation in the study area is 43 cm. The mean annual air temperature for the site is 3.8° C, with the frost-free period of less than 60 days. Much of the annual precipitation comes in the form of snowfall between October and April.

The site was selected because it contained numerous, undisturbed ant nests, and the soil was relatively homogeneous. Additionally, observations by the land owner were useful in determining the ages of the nests. There were 41 nests in the study area, three of which were abandoned.

Ant Biology.—Observations of ant behavior and ecology (foraging, caste structure, feeding habits, myrmecophiles, brood dynamics, etc.) were made for 10 h weekly from May through September, 1988. To obtain an accurate sample of the ants for description and estimates of biomass, a 3199 cm^3 core was taken of three small (< 75 cm in length), medium (76 to 126 cm in length) and large (> 126 cm in length) nests. Population counts included eggs, major and minor workers (females and males). Using the census of the core samples of known volume, total populations were extrapolated on the basis of the estimated nest volume.

Ant Nests.—All nest dimensions were taken (length, width, and height), and nearest neighbor distances between nests were measured. Nest and thatch area/volume were calculated after the nests selected for core studies had been excavated and their interior construction was revealed. Nest entrances were counted on 23 of the 38 viable nests. To estimate the volume of the nests, without excavation, formulae were devised to fit the unusual dimensions of the nests. The nests were divided into three sections: the ellipsoid surficial mound (volume = $0.5 \times [4.19 \times (\text{height}) \times (\text{length}/2) \times (\text{width}/2)]$), the vertical below ground cylinder (volume = $3.14 \times (\text{length}/6)^2 \times [(2 \times \text{height}) - (\text{length}/6)]$), and the sphere of soil–thatch contact (volume = $0.5 \times [4.19 \times (\text{length}/6)^3]$). The total nest volume was estimated from the sum of these three sections.

Material collected from the cores was separated with regard to soil and vegetation. The amount (volume and weight) of air, thatch, soil (< 2 mm) and gravel (> 2 mm) was determined. To assess the contribution of thatch to nest volume, the vegetation was first ground into a fine powder. Differences in the composition of nest and adjacent soil were analyzed with a χ^2 test of proportions (Siegel 1956).

Soil.—Eight nests were selected for soil analysis, including three small (< 75 cm in length), two medium (76 to 126 cm in length) and three large (> 126 cm in length) nests. The nests were cored directly through the center with a 10 cm diameter soil corer and hand spade. Soil and thatch were collected from the nest for analysis. The depth in the nest to which cores were taken was dictated by the depth of the adjacent soil core taken 1.5 m from each nest. The adjacent soil core was was taken on the side of the nest that was not used for foraging paths by the ants. In all samples, the depth of both nest and off-nest coring was 60 cm, the minimum soil depth at the study site.

Soils were sampled at 10 cm intervals to detect variations in chemical and physical changes as a result of ant habitation, as suggested by Baxter and Hole (1967) and Salem and Hole (1968). Following the traditional soil horizon designators would have accomplished very little, due to the alteration of the horizons by the ants. Samples were returned to the laboratory where thatch, soil (< 2 mm) and gravel (> 2 mm) were separated for volume and weight per unit volume analyses. Thatch was separated from the soil and gravels by sieving and flotation. Particle sizing was done by the pipet method (Gee & Bauder 1986), fraction percentages being broken down into clay (< 2 μm), silt (2 to 50 μm), and sand (50 μm to 2 mm).

From the corings, soil bulk density, soil moisture, and soil porosity were determined for the 10 cm increments to assess the physical alterations on the soil by the ants. Bulk density measurements were taken using the clod method (Archimedes' principle, Gee & Bauder 1986). Soil moisture was determined by oven drying 50 g of fresh field soil at 105° C and determining weight loss after 12 h. Soil porosity was calculated from the known bulk density, assuming a particle density of 2.65 mg/mm^3 (Gee & Bauder 1986). Soil pH (1:1 paste) readings were taken on the nest and control soils with an electronic pH meter.

Nest, air and adjacent soil (10 cm depth) temperatures were taken for eight viable nests (five with brood and three without) on 2 September. On 16 September (the day after a killing frost) nest, air and soil temperatures were taken for eight live and five dead nests. On 10 December (the day after a snowfall of 14 cm) nest, air and soil temperatures were taken for seven live nests. Differences in the temperatures of the nests, air and soil were assessed with Fisher's protected least significant difference post-ANOVA test (Steel & Torrie 1980).

Results and Discussion

Ant Biology.—The major workers were recognizable by their bicolored appearance; the head and thorax were dull red, with a black gaster. The minor workers, which included most of the brood workers, were smaller in size and were usually entirely black. Major workers were 6.4 ± 0.4 mm long and weighed 3.0 ± 0.7 mg; minor workers were 4.8 ± 0.3 mm long and weighed 1.0 ± 0.2 mg. Females had a red-brown head and thorax, with a black gaster and were 7.6 ± 0.3 mm long and weighed 9.0 ± 4.0 mg. Male reproductives were completely black and were 7.4 ± 0.2 mm long and weighed 10.0 ± 2.0 mg. Male reproductives first appeared in the nests on 2 June. Eggs averaged 4.0 ± 1.1 mg, and larvae in early June were 0.86 ± 0.31 mm long and weighed 36.0 ± 8.0 mg.

The small nests had 9000 to 15,000 ants; medium sized nests had 17,500 to 37,000 ants, and large nests had 53,000 to 66,500 ants (Table 1). Very few male

Table 1. Population parameters ($\bar{x} \pm$ SE) for small (length < 75 cm), medium (length 76–126 cm) and large (length > 126 cm) nests of *Formica obscuripes.*

		Reproductives		
Nest size	Workers	Female	Male	Eggs
Small	11,276 ± 1858	35 ± 32	0 ± 0	1523 ± 680
Medium	24,403 ± 6433	56 ± 31	7 ± 4	342 ± 178
Large	59,831 ± 6788	14 ± 14	1 ± 1	2008 ± 359

reproductives were found in medium and large nests, and no male reproductives were found in the small nests. These population estimates are somewhat larger than those derived by Sather (1972) but support his conclusion of a positive correlation between nest size and population. The largest nests had few female reproductives, compared to small and medium nests. Large numbers of eggs were found in all nests, except one medium nest that had none.

The only foods used by the ants during the study were insects, especially beetles. The primary beetles found in the ant nests were carabids, curculionids, and two species of tenebrionids: *Embaphion muricatum* Say and *Eleodes opaca* Say. There were several varieties of seeds found in the nests, but it is not clear whether these were simply additional building materials or foodstuffs.

The only myrmecophiles found in the nests were dermestid larvae. Because these larvae feed on organic refuse, it is not unusual that they should be found in the nests of *F. obscuripes,* which are nutrient-rich reservoirs with plant roots, eggs, and insect carcasses. Aphids were frequently present on vegetation adjacent to the nests. The minor workers from the nest were often found with the aphids on vegetation, possibly harvesting honeydew (Gregg 1963).

Foraging paths radiated out from the mound center covering a swath of ca. 300°. When within 20 m of another nearby mound, the foraging patterns always maintained a vacant zone which foragers from neither nest entered. Occasionally foragers from different nests encountered one another, which usually resulted in aggressive interactions. Foraging paths of several mounds were measured and averaged 4.0 ± 0.6 cm in width. The larger the nest, the longer the foraging paths, with the average path length for all nests being 15.7 ± 1.2 m. Practically all foraging paths were highly branched and terminated in a branched fan. Foraging paths were used for conveying food and thatch back to the nest.

Ant Nests.—All of the nests at the study site were in open areas, devoid of cover. The ant nests appeared to be nutrient-rich centers; around each nest, and occasionally on the nest, were thick growths of grasses and other vascular plants. All excavated nests were found to contain the base and roots of small plants, usually sagebrush (*Artemisia* spp.). With the exception of younger nests (< 2 years), all surficial traces of the sagebrush were absent. Contrary to Cole's (1932) observation that the ants completely destroyed the sagebrush plant, sagebrush roots were found in most nests. The root in all cases had the epidermal layer stripped, leaving the cambium layer exposed. The younger nests with the sagebrush plant still intact rarely exceeded 5 cm in height. Some excavated roots were hollowed out and used for passages within the nest. It is doubtful that the ants ever completely remove the sagebrush root, because of the stability and anchorage it provides for the nest. One locale near the western slope of the Laramie Range,

Table 2. Physical characteristics of nests of *Formica obscuripes.*

Parameter	Minimum	Maximum	Mean ± SD
Nest length (cm)	52	151	95 ± 23
Nest width (cm)	48	128	84 ± 20
Nest height (cm)	11	36	21 ± 5
Nest volume (m^3)	0.14	0.65	0.25 ± 0.09
Nest entrances	5	65	22 ± 15
Nearest neighbor (m)	8.84	51.21	28.92 ± 10.34

with sagebrush and saltbush (*Atriplex* spp.), has no visible mounds but is occupied by *F. obscuripes* living in the root systems of the shrubs.

In the study area, nests averaged 95 × 84 × 21 cm and had an average volume of 0.25 m^3 (Table 2). The uniform distribution of nests suggested a territorial dispersion, although previous work has suggested a more clumped distribution (Sather 1972). However, the size of the territory was not based on nest size; there was a coefficient of correlation of only 0.106 ($n = 38$, $P > 0.10$) between nearest neighbor and nest size. Nearest neighbors at the study sight averaged 28.9 m and ranged from 8.8 to 51.2 m between nests (Table 2). Previous research (Weber 1935) has indicated that *F. obscuripes* does not have mating flights like other ant species; rather, reproductives leave the nest slowly over a period of several weeks. This may contribute to a high density of nests in a given area.

The nest of the thatching ant was composed primarily of dead vegetation collected from the surrounding habitat, but also included substantial amounts of soil and gravel. Previous studies have implied that the nests were entirely thatch (Sather 1972). The composition of the nest soil differed significantly ($P < 0.05$) from that of the surrounding soil. At no time during observations did foragers bring fresh vegetation to the nest. The nests also contained feces from the Wyoming ground squirrel (*Spermophilus elegans* Kennicott), Mountain cottontail (*Sylvilagus nuttalli* Allen), and the Plains Harvest mouse (*Reithrodontomys montanus albescens* Carey). Interestingly, no feces of the Blacktail prairie dog (*Cynomys ludovicianus ludovicianus* Ord) were found in the nests although there were several, active prairie dog colonies in the study area.

The mounds were elliptical domes (Sather 1972), with the outer 25% of the ellipsoid dome rim resting on a built-up portion of soil. The thatching material of the nests extended beneath the ground forming a cylinder that terminated in a rounded end which enjoined with the soil. The thatching material extended into the ground a distance of approximately two times the height of the nest above ground (Fig. 1).

The soil that formed the rim beneath the elliptical dome probably came from the excavated hole that contained the thatch, as there was no indication of discarded or excavated material elsewhere near the nests. The vertical limitations of the construction with thatch beneath the ground was found to be approximately 60 cm, due to a lithological contact (Sherman granite) which ranged from 60 to 90 cm throughout the area. Although most nest dimensions were comparable to Sather (1972), our work suggested that a greater proportion of the nest was underground.

Soil was found throughout the thatch, which meant the ants did not completely

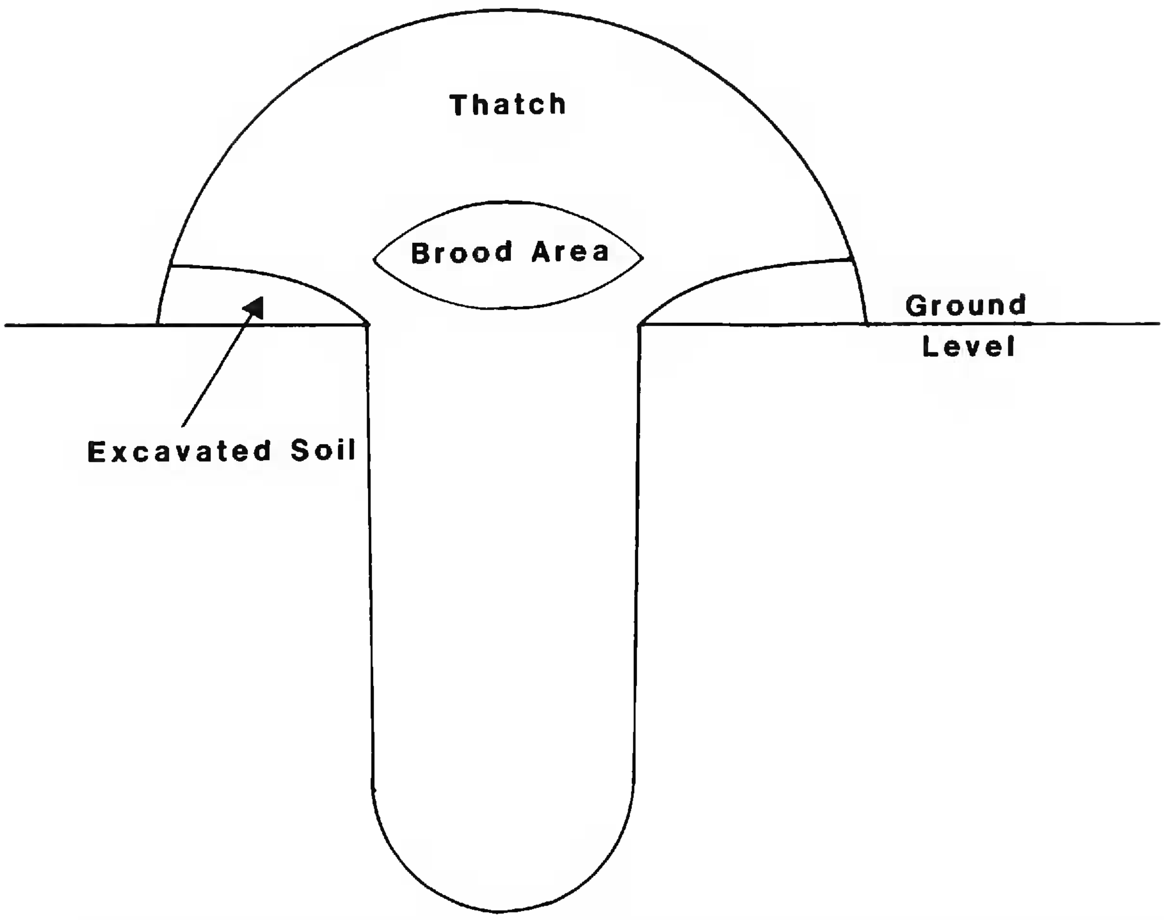

Figure. 1. Schematic representation of a typical nest of *Formica obscuripes* showing the relationships between the nest dimensions and location of brood.

abandon it as a construction material. Thatch used in the nest construction was between 1 and 10 cm in length ($\bar{x}$ = 3.4 ± 2.1 cm, 33.4 ± 10.2 mg), and rarely exceeded 0.5 cm in diameter. The number of entrances into the mound ranged from 5 to 65 ($\bar{x}$ = 22 ± 15) and were generally associated with the nest size (Table 2). Most of the entrances were through the thatch, although some passed through the soil which rimmed the mound. Contrary to the observations of Cole (1932), the main brood chambers were not located 1 m beneath the ground surface of the nest, but between 10 and 20 cm below the apex of the mound. This was found to be the case with every nest excavated, and this observation corresponds with the work of Weber (1935). The brood was probably located in the center of the nest to facilitate ventilation and moisture control, as the soil in the study site was prone to increasing moisture with soil depth.

The nests constructed by *F. obscuripes* are apparently able to regulate temperature. Sather (1972) noted that most nests were located in shady areas, but those in sunny areas were apparently oriented for efficient solar collection. Our observations revealed that the ants periodically opened and closed entrances and may thus be able to regulate air flow and nest temperature. However, when temperature readings were taken from September to December, it became apparent that something other than regulated air flow was controlling the nest temperature. On 2 September, nest temperatures were significantly ($P < 0.05$) warmer that air temperatures, but only if eggs were in the brood area (Table 3). Ground temperature was significantly ($P < 0.05$) lower than either the air or nest temperature. On 16 September, the air temperature was significantly ($P < 0.05$) warmer than the nest temperatures, and there were no eggs in any of the nests (Table 3). However, in all but one case, the nests were still significantly ($P < 0.05$) warmer than the ground. Temperatures of dead nests provided the same relative differences

Table 3. Temperatures of air, ground and *Formica obscuripes* nests with time.

Date	Air (°C)	Ground (°C)	Nest (°C)	Eggs	Condition	*n*
9 Sep	19.5	16.0	18.7	absent	live	3
9 Sep	18.8	16.8	21.8	present	live	5
16 Sep	11.4	5.4	8.7	absent	live	8
16 Sep	13.1	6.1	10.6	absent	dead	5
10 Dec	−1.9	−3.2	−1.1	absent	live	7

with respect to ground and air temperature as those that were occupied by ants. In dead nests, the air temperature was significantly ($P < 0.05$) warmer than the nests, which were significantly ($P < 0.05$) warmer than the ground surface. This indicated that the nests were constructed in such a way as to trap solar radiation in the nesting material or harness the heat of decomposition of thatch or other organic matter in the nest. On 10 December, the ground temperatures were significantly ($P < 0.05$) colder that either the nest or air temperatures (Table 3). The nest temperatures were slightly warmer than the air temperatures, which indicated that the nests were effectively collecting solar radiation, since little decomposition would have been taking place in such cold temperatures. This warming capacity was further demonstrated by snow melting first from the nests, exposing them several days before the ground was visible. The process of solar heating may have been augmented by a high thermal absorbance and low thermal diffusivity of the

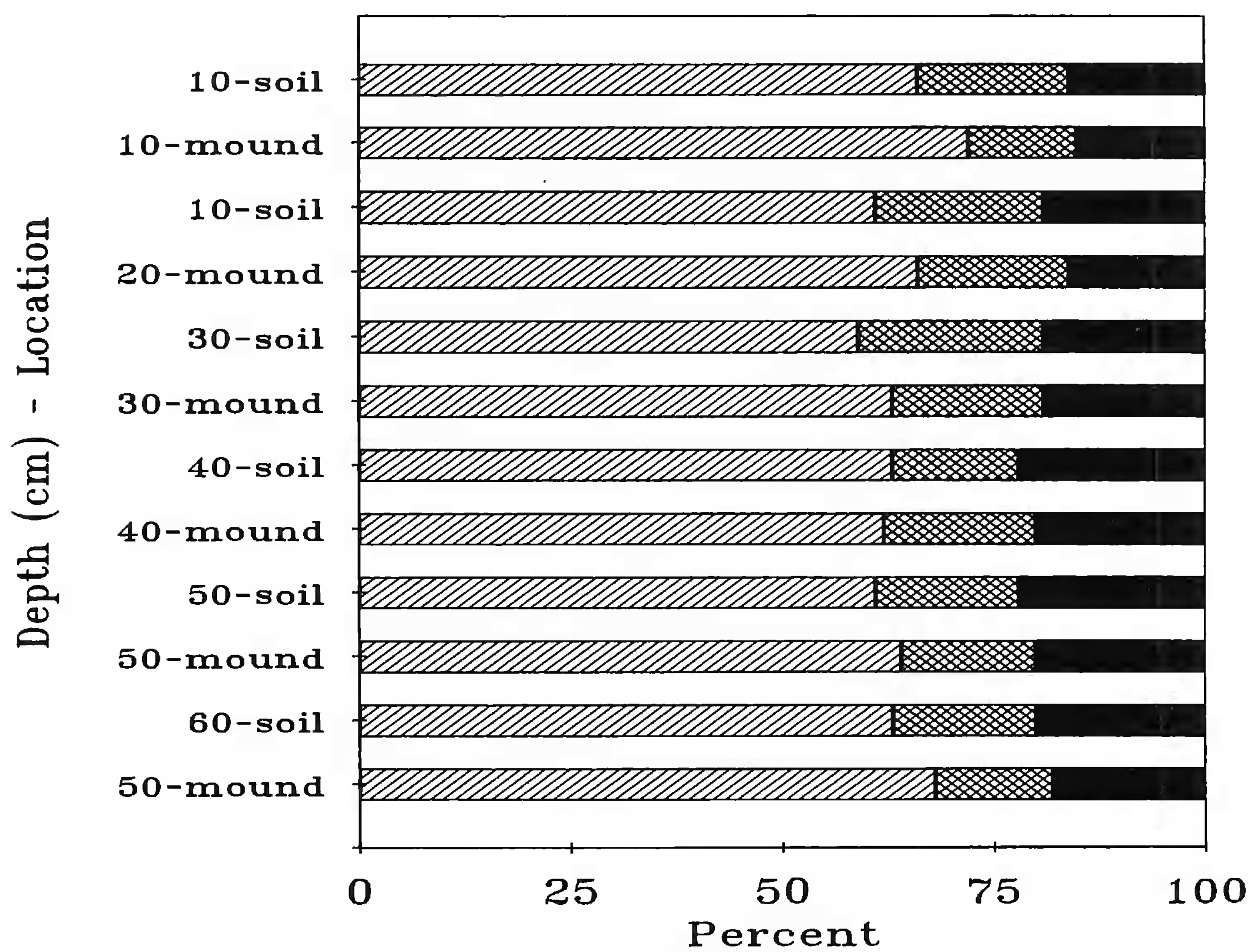

Figure 2. Amount of sand (stripped), silt (cross-hatched) and clay (black) in the soil as a function of depth within and adjacent to nests of *Formica obscuripes*.

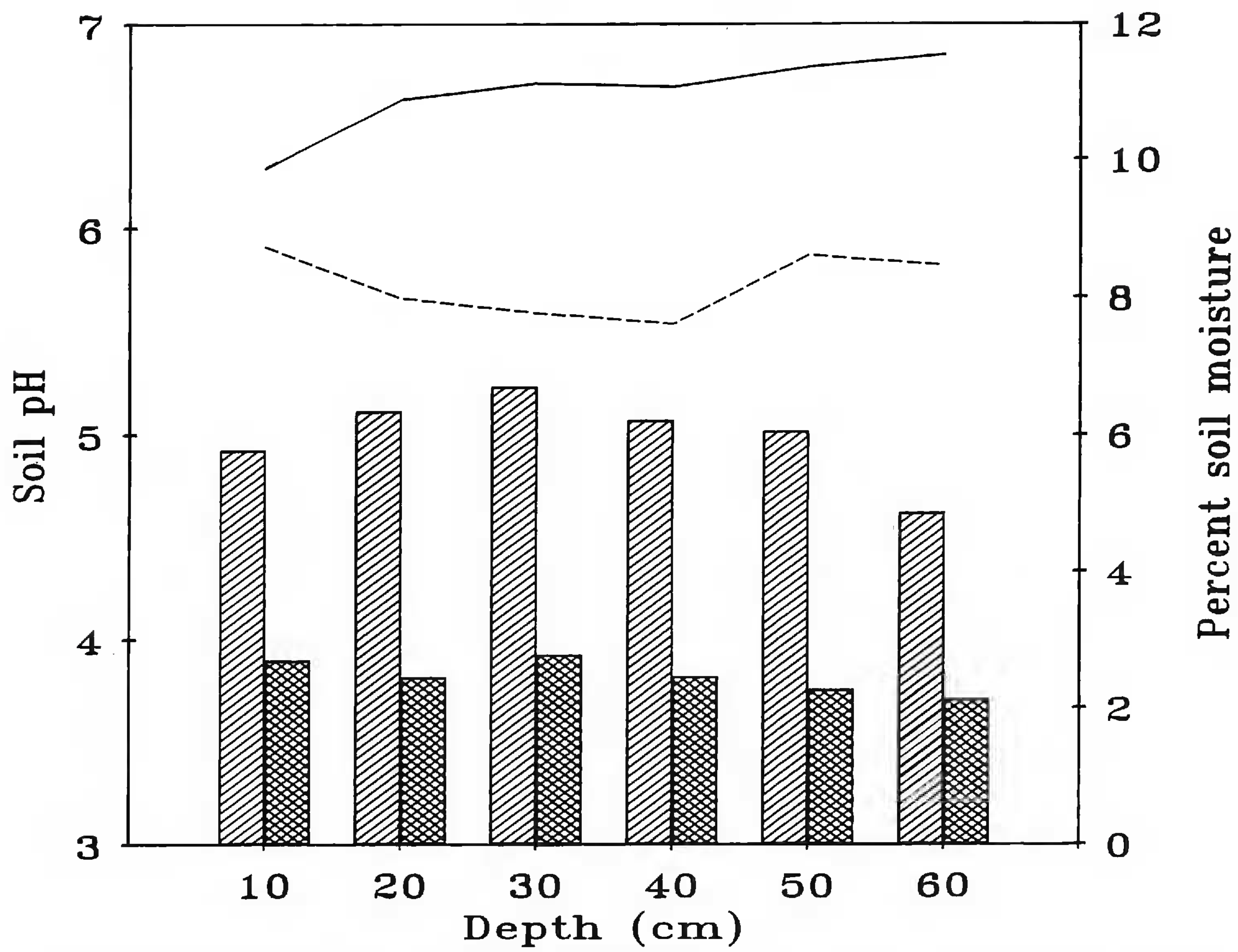

Figure. 3 Soil moisture (stripped = adjacent, cross-hatched = within) and pH (solid line = adjacent, dotted line = within) as a function of depth within and adjacent to nests of *Formica obscuripes*.

nesting materials. It is particularly intriguing that the ants selectively retained materials in the nest with low thermal diffusivity and discarded materials with poorer thermal properties (e.g., sand has a thermal diffusivity of 0.003, as compared to gravel and granite with thermal diffusivities of 0.008 and 0.016, respectively [Sabins 1987]). Thus, the inorganic materials selected by the ants for nest construction had better heat retention properties than a random or representative selection of the available materials.

Soil.—Soils in the study site were brown to dark brown (7.5 YR 5/4, 3/4 on the Munsell soil color index) sandy loams and sandy clay loams with colors of 7.5 YR. In those locations where the soil was a sandy clay loam, the ants altered the texture to a sandy loam. In all the ant nest soils, the texture of the soil was a sandy loam, even if the adjacent control soil was a sandy clay loam. An anomaly of sand and silt ratios was found in all the nests sampled between 25 and 45 cm (Figs. 2 and 3). This phenomenon can be explained by the presence of the brood centers, because the brood was always somewhere within this depth range. The ants may have altered the amount of sand and silt at this depth to facilitate the movement of water through the center of the nest and thereby reduce moisture retention in the brood area.

When constructing nests, ants displaced most of the soil with thatch, leaving large gravels (> 3 mm) in place. The soil left in the nests had an altered composition (Table 4); sand was retained but enough silt and clays were removed to change the soil texture from that found in soil adjacent to the nests (Fig. 2). From

Table 4. Composition of *Formica obscuripes* nests and adjacent soil by weight and volume.

Substance	Weight (%)			Volume (%)		
	Thatch	Soil[a]	Gravel[b]	Air	Thatch	Soil/gravel
Soil/gravel	0.0	20.9	79.1	0.0	0.0	100.0
Nest (small)	39.3	34.9	25.8	47.4	38.2	14.4
Nest (medium)	44.1	38.9	17.1	49.8	39.7	10.5
Nest (large)	48.8	31.1	20.1	46.5	44.2	9.3

[a] Soil includes particulates < 2 mm.
[b] Gravel includes particulates > 2 mm.

observations of nests under construction, it appeared that a sagebrush root afforded a channel beneath the ground in which to start replacing soil with thatch. When the thatch accounted for a majority of the nest volume, channels or tunnels were excavated in soil surrounding the thatch core. This soil was displaced with thatch, helping to expand the nest laterally and consequently expanding nest volume. The unwanted clays, silts and sands were removed to an area surrounding the surficial cavity opening, and built into a rim which rested beneath the thatch dome.

The ants have a marked influence on the physical characteristics of the soil. There was a higher porosity and lower moisture content in the nest soils than in adjacent soils. The ants also slightly altered the color of the soil. Soil color beneath a nest was more homogeneous than in adjacent cores, as a result of the ants selectivity using one soil particle size over another in the nest. The pH readings indicated a considerable alteration of the soil, either by the ants or decaying vegetation. The pH levels were considerably lower in the nests than in adjacent soil (Fig. 3). In addition, while the ants limited the soil moisture within the nests (Fig. 3), they apparently needed accessible moisture in surrounding soil. Nests found in the Laramie Basin tend to be on river terraces with high water tables, or on foothill slopes where there is sufficient runoff and intergrades of Aridisol and Mollisol soils. *Formica obscuripes* is a highly adaptive ant, as evidenced by its expansive geographical distribution (Gregg 1963). Its ability to construct a nest that apparently mediates temperature and moisture may contribute to its spread on this continent. In addition to its regulation of microenvironmental factors, *F. obscuripes*' use of thatch in its nest effectively concentrates available nutrients, thereby promoting localized primary production and prey density, with the apparent result of enhancing its own food supply.

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